time was too short to permit of sending a delegate to attend the anniversary.

The deaths of Prof. Othniel Charles Marsh, of New Haven, on March 18, in his sixty-eighth year; of Richard A. Tilghman, of Philadelphia, on March 24, in his seventy-fifth year, were announced.

On motion of Mr. Prime, Gen. I. J. Wistar was appointed to prepare an obituary notice of Mr. Tilghman.

A paper was read on "Specializations of the Lepidopterous Wing: The Parnassi-Papilionidæ, II," by A. Radcliffe Grote, A.M.

The Society was adjourned by the presiding officer.

SPECIALIZATIONS OF THE LEPIDOPTEROUS WING: THE PARNASSI-PAPILIONIDÆ.

II.

(Plates III, IV and V.)

BY A. RADCLIFFE GROTE, A.M.

(*Read April 7, 1899.*)

Fam. III. Papilionidæ.

The cubital cross-vein is always distinct, while in certain forms it does not connect inferiorly with vein vii, but is arrested at the submedian fold (vein vi). This latter is bent downwards to vein vii, beyond the cross-vein, in those types in which the cross-vein attains vein vii (see Comstock's figure in *Evolution and Taxonomy*, Plate ii, Fig. 2), and appears again within the cross-vein to base of wing. In certain forms the submedian fold is continuous from base to external margin, and the cross-vein then rests on this fold and does not reach vein vii (*e. g.*, *Eurycus cressida*, *Pathysa antiphates*, *Iphiclides podalirius*). The following table separates neurational groups, and, as far as possible, the genera. The hairy male pockets on the hind wing I have not specially examined. In the nomenclature of the veins I continue to follow Comstock.

1. Vein iii_3 of primaries out of iii_4 beyond the cell halfway to apex:
   2. Cell of hind wings disproportionately reduced:
      Hind wings greatly developed inferiorly, with long, pointed tail.....(1st Group) *Leptocircus.*
1. Vein iii_3 of primaries arises from radius more or less exactly opposite to the point of junction of discal cross-vein:
   2. Cell of hind wings subequal, narrowed outwardly by a downward curve of cross-vein between iii and iv_1:
      3. Vein iii_1 of primaries anastomoses with ii:
         Hind wings produced inferiorly, with short, sharp tail... (2d Group) *Idaides.*
         Hind wings produced inferiorly, terminating bluntly, without tail.....*Zetides.*
         Hind wings not produced inferiorly, rounded, tailless... *Arisbe.*
         Hind wings not produced inferiorly, with long, narrow, equal tail.....*Pathysa.*
   2. Cell of hind wings subequal, not narrowed outwardly (except in *Iphiclides*):
      3. Vein iii_1 of primaries free to costa:
         4. Internal vein of hind wings shorter, running out on internal margin before the longer excision at anal angle:
            Hind wings tailless.....(3d Group) *Eurycus.*
            Hind wings tailed.....*Pachlioptera.*
         4. Internal vein of hind wings longer, attaining the internal margin before the shorter excision at anal angle: (4th Group)

[*Papilio, Iphiclides, Jasoniades, Euphoeades, Heraclides, Laertias, Menelaides, Achillides, Orpheides, Nestorides, Calaides, Priamedes, Parides, Ithobalus, Iliades, Troilides,* with the types given by Scudder, I am unable to separate by adequate neurational or wing characters in a table. They all generally agree, most of them exactly except by relative characters so obscure as to be of hardly more than specific value.]

1. Vein iii_3 arises from radius above the cell and just before the junction of the cross-vein.....(5th Group) *Trogonoptera.*
1. Vein iii_3 arises from radius above the cell and well before the point of junction of discal cross-vein:

4. Internal vein of hind wings reaching to anal angle, internal margin full and rounded.....
(6th Group) *Ornithoptera.*

From the foregoing table we may extract the following neurational diagnoses of the principal genera in the different groups:

(1st Group.)

Gen. *Leptocircus* Swainson, 1832.

Type: L. curius.

= *Lamproptera* Gray, 1832 (preoccupied).

Vein iii_3 of primaries arises out of iii_4 beyond the cell halfway to apex of wing. Cell of hind wings disproportionately small and reduced. Hind wings greatly developed inferiorly, with long, pointed tail. On primaries the cubital cross-vein does not attain vein vii, but is arrested at submedian fold (vein vi). Vein "ix" of primaries present, as everywhere in the Papilionides.

The neuration of primaries, owing to the advanced position of vein iii_3, presents very striking analogies with the Sphingidæ, but a relationship with this group is absolutely excluded by the presence of vein "ix" and absence of viii on fore wings. An habitual resemblance to *Goniloba* and other Hesperian genera is offered by the coloration; this is perfectly contradicted by the neuration which is Papilionid. How great must be the phyletic value of vein "ix," if it persist in this isolated and aberrant form! In none of the generic types examined by me do I find any probable indications of the more immediate phylogeny of *Leptocircus.*

(2d Group.)

Gen. *Idaides* Hübner, 1816.

Type: I. codrus.

Vein iii_3 of primaries arises from the radius more or less exactly opposite the point of junction of the discal cross-vein. The discal cell of secondaries is subequal, but is narrowed outwardly by a downward curve of the cross-vein, between radius (iii) and first branch of media (iv_1). Vein iii_1 of primaries, the first radial branch, anastomoses with vein ii. The cubital cross-vein is degenerate, narrow, and does not reach vein vii. The hind wings are produced inferiorly, and vein iv_2 terminates in a short and sharp tail.

This term has priority for a well-defined group characterized by the junction of the first radial branch with the subcosta. It is also marked by the downward scoop of the cross-vein between veins iii and iv_1 on hind wings. The genera *Idaides* and *Zetides* are closely allied, and appear merely to differ by the details of specialization of the outer margin of secondaries. *Arisbe* stands further apart by the rounded, not produced, hinder margin of secondaries. It possibly represents an older form of the group. *Pathysa* differs by the frail, testaceous veins, as well as by the tailing of the normally proportioned hind wings. In all of these characters, as well as in the striped ornamentation, it recalls *Iphiclides*, belonging to a different group having vein iii_1 free to costa. A further character, and one which suggests that *Iphiclides* presents an intermediary type, is that this latter genus has also the cross-vein of secondaries downwardly curved, between radius and first branch of media on hind wings. The intersection of the radial branches with the subcosta, which characterizes this group, is paralleled in the Charaxinæ. Nevertheless, I think we cannot regard this common feature as indicating more than an analogy between the Nymphalids and Swallowtails.

(3d Group.)

Gen. *Eurycus* Boisduval, 1836.

Type: E. cressida.

Vein iii_3 of primaries arises from the radius at a point more or less exactly opposite that of the junction of the discal cross-vein. The discal cells are subequal on both wings. Vein iii_1 of primaries free to costa. Internal vein of hind wings shorter, running out on internal margin before the long excision at anal angle. On primaries the cubital cross-vein expires just before vein vii. Humeral cell of secondaries large, subquadrate. Hind wings subovate, without tail.

This group is interpolated in this place on account of the extreme specialization of internal margin of secondaries and the shortening of vein vii. Thus the same tendency is manifested here as in the Parnassiidæ, to hollow out the margin and shorten the anal vein of the hind wings. The group is probably a lateral specialized branch from early forms of the succeeding and more typical group of the family. The genus *Pachlioptera* Reakirt, 1864, with the type *aristolochiæ*, differs very slightly. I regret not to have been able to examine *Blakeia gundlachianus* (columbus, grotei).

(4th Group.)

Gen. *Papilio* Linné, 1758.

Type: P. machaon.

Vein iii_3 arises out of radius more or less exactly opposite to the point of junction with discal cross-vein. Cells subequal. Vein iii_1 of primaries free to costa. Internal vein of hind wings inwardly curved, attaining the margin just before the short excision at anal angle. Cubital cross-vein joins with vein vii.

Except *podalirius*, the types of the genera arranged under this rubric agree in main features, while differing in small details which it is optional to consider as of generic value. In *machaon* the humeral cell of hind wings is small and narrow. The præcostal spur has a lateral extension. There is a moderate, narrow tail, not spatulate.

(5th Group.)

Gen. *Trogonoptera* Ripp., 1890.

Type: T. brookeana.

Vein iii_3 arises just before the point of junction of cross-vein with radius. Cubital cross-vein not attaining vein vii. Fore wings long and narrow, pointed, entire. Hind wings reduced, rounded, tailless. Internal margin full, the vein straight, continuous. From the characters of the radius this genus is nearer to *Papilio* than to *Ornithoptera*. It is remarkable how persistent the neurational features are in the group of *Papilio*, and especially that vein iii_3 is so immovable in its position nearly exactly opposite the cross-vein. It must be therefore considered an important feature that this vein arises much beyond the cross-vein in *Leptocircus*, and before it in *Ornithoptera*. In *Trogonoptera brookeana* it has not quite attained the Papilionid position, but it has decidedly abandoned that of *Ornithoptera*. The structure of the hind wings resembles that of the latter genus.

(6th Group.)

Gen. *Ornithoptera* Boisduval, 1832.

Type: O. priamus.

Vein iii_3 arises out of radius above cell and well before the point of junction of cross-vein. Discal cells subequal. Vein iii_1 free to costa. Internal vein of hind wings reaching anal angle; no anal excision.

The comparative characters are those of generalization, so that *Ornithoptera* presents features which the rest of the Papilionides have probably abandoned. In the same way I assume that the species of *Eurymus* (*Colias* Auct.) have passed through a *Meganostoma* stage, and the entire extant Pieridæ an *Anthocharis* stage, in which latter the Radius was five-branched and generalized. There is a strangeness about *Ornithoptera*, suggesting a separate origin. This disappears with the higher forms of the Papilionides, which have come to look much like other butterflies. The remaining generic types may be now gone over in review. As far as possible I take the generic titles in their chronological order.

(2d Group.)

Zetides sarpedon.

Agrees with *Idaides*, except that the secondaries are bluntly produced inferiorly and are without a tail. Vein iv_2 lies somewhat nearer iv_3 at base. In both genera the excision at anal angle is long, owing to the produced wing, but vein vii is not relatively shorter, as in *Eurycus* (3d Group). *Zetides* appears more specialized than *Idaides*. The differences are small, but may be considered as of generic importance.

Arisbe similis.

Agrees with *Idaides*, except that the secondaries are not produced inferiorly; the outer margin is rounded, without salient projection. The anal excision is shorter. The position of iv_2 on secondaries is more central, and this appears a more generalized form than either *Idaides* or *Zetides*.

I am indebted to the kindness of Dr. Karl Jordan for material of this species. Notwithstanding the differences in shape of hind wings, these three genera are undoubtedly phylogenetically nearly related. The veins are opaque and strong.

Pathysa antiphates.

Agrees in one essential neurational feature, the fusion of the first radial branch, with the preceding genera, to which, notwithstanding "superficial" discrepancies, it may thus be distantly related. The cubital cross-vein is attenuate, and does not reach vein vii. On the secondaries the position of iv_2 is nearly central. Vein iv_3 is produced into a long tail, not spatulate. In shape of wing this genus resembles *Iphiclides*, as also in the slender, transparent

veins, and in the striped character of the ornamentation. It probably occupies an independent intermediate position. The colors in this group, brown and greenish yellow, are peculiar, and, in preparing the wings in the usual manner, they are persistent. *Pathysa* has striped wings. In *Arisbe* the bands are indicated by scattered blotches. These latter are gathered into a single series of interspaceal spots in *Idaides*, on the primaries. These spots coalesce and broaden into a band, which also obtains over the hind wings, in *Zetides*.

The coincident characters of *Pathysa* and *Iphiclides* allow of no other conclusion than that the two are somewhat nearly phylogenetically connected, notwithstanding the fact that in *Pathysa* the first branch of radius joins subcosta, while in *Iphiclides* it is free. Assuming that the Second Group contains younger forms, we might have in *Iphiclides* a type representing a stage through which *Pathysa* has already passed. But *Iphiclides* and the members of the Second Group are in one character more generalized than *Papilio* and its immediate allies, *i.e.*, the straight internal vein of hind wings. We have probably to do with divergencies from a common stock in different directions, in part retaining characters of generalization. It is sufficient here that we show that *Iphiclides* and *Papilio* constitute totally distinct genera, having probably a different immediate ancestry. And it remains a possibility that the fusion of the first radial branch with subcosta is a more recent feature, here engrafted upon a wing in other characters representing an older type than *Papilio*. Thus the *Idaides* group may be a lateral branch, thrown off before the tendency of the internal vein to curve and shorten on hind wings was developed. And to this branch, as represented by *Pathysa*, *Iphiclides podalirius* and allies may be related. In respect of the curved inner margin of the hind wings, *Papilio machaon* and allies are more specialized than *Iphiclides*.

(3d Group.)

Pachlioptera aristolochiæ.

The shape and neuration of primaries agree exactly with *Eurycus*, except that the cubital cross-vein, while narrowing inferiorly, appears to reach vein vii, forcing the submedian fold down to the vein. On secondaries the humeral cell is smaller and vein iv_3 terminates in a spatulate tail. Veins iv_2 and iv_3 are not so near at

base as in *Eurycus*, than which this form appears more generalized. I do not doubt the validity of the genus.

(4th Group.)

Iphiclides podalirius.

Compared with *Papilio machaon* the veins are more slender and transparent. Veins iv_2 and iv_3 on secondaries are nearer together at base. The internal nervure is straight and the margin fuller on hind wings. On primaries the cubital cross-vein is slighter and does not attain vein vii. The discal cross-vein is downwardly curved on hind wings between iii and iv_1. The humeral cell is larger than in *Papilio*.

By the free first radial branch this genus agrees with *Papilio* and the other genera of the group. Otherwise it is more nearly connected with *Pathysa antiphates*, and its generic distinction as compared with *Papilio* is beyond question. The straight internal vein of secondaries is a character of generalization as compared with *Papilio*.

Jasoniades turnus.

Agrees very closely with *Papilio*. The humeral cell is larger, the tail shorter and a little spatulate. The internal vein is curved, as in *Papilio*, with which it so closely corresponds as to make the propriety of its generic separation doubtful. The two forms appear to belong to the same immediate phylogenetic line.

Euphœades troilus.

The tail is a little shorter and spatulate; otherwise this form agrees so exactly with *Jasoniades* that I find no distinguishing character whatever. Belongs to the same branch and group.

Heraclides thoas.

The tail is a little longer than in *Jasoniades* and spatulate. Vein iv_2 on secondaries is a little farther from iv_3, so that *Heraclides* is more generalized. Otherwise I find no differences whatever. From *Euphœades* I find only the slightly longer tail to distinguish it.

The separation of the preceding forms, except *Iphiclides*, from each other and from *Papilio* seems difficult from the neuration. All have the internal vein of secondaries curved and are evidently very nearly related, belonging to the same phyletic branch of the family.

Laertias philenor.

Agrees with *Papilio* and preceding genera, except that the internal vein of secondaries is straighter and the margin fuller. I think this feature important. The tail is shorter and hardly spatulate. While otherwise resembling *Jasoniades*, the relative position of iv_2 is a little more removed from iv_3 at base. Appears a slightly more generalized type than any of the foregoing, and to represent a stage from which it is probable the preceding (except *Iphiclides*) have emerged.

Menalaides polytes.

Differs from *Laertias* only in that the tail is shorter and broader, somewhat spatulate.

Achillides paris.

Agrees with *Laertias* and *Menalaides*, except that the humeral cell narrows a little more outwardly. The tail is a little longer than in *Menalaides*, from which I cannot otherwise satisfactorily separate it. These three "genera" appear to be related by the straighter vein vii of secondaries.

Orpheides demoleus.

Appears nearest related to *Jasoniades*. It only differs by the absence of a tail, and in that the præcostal spur is continued, in an even curve, quite to the shoulder of the wing. The internal vein of hind wings is bent as in *Jasoniades* and allies, with which it should be apparently associated.

Nestorides gambrisius.

Not distinguishable structurally from *Orpheides demoleus*. The præcostal spur is equally continuous, and, although the proportions of the humeral cell are very slightly different, I am of opinion that no sufficient generic characters can be supplied by the neuration.

Calaides androgeus.

Agrees well with the preceding, but differs by the median and cubital branches of the hind wings forming sharp projections, of which that to iv_3 is, as usual, the longest. On primaries vein iii_3 yields very slightly to the tendency to be outwardly removed, and arises beyond the exact point of junction of cross-vein.

The following three generic types stand rather apart and by themselves. There is, except the straighter anal vein, nothing in

the neuration to contradict main features in the definition of *Papilio*. They appear, on the whole, to be somewhat generalized forms, from the usually straight internal vein of hind wings.

Priamides pompeius.

Primaries rounded at tips; outer margin even, medially hollowed out, so that the wing may be described as subfalcate. Cubital cross-vein continuous to vii. Secondaries with præcostal spur continued to the margin, humeral cell moderate, internal vein somewhat bent, no tail, outer margin regularly scalloped.

Ithobalus polydamus.

Agrees with *Priamides* in shape of primaries, outer margin a little scalloped. Secondaries with internal vein straight, outer margin as in *Priamides*. Præcostal vein shorter, not reaching margin.

Parides echelus.

Primaries pointed, with sharp tips; external margin even, nearly straight. Hind wings with the outer margin produced between iv_2 and v_2, scalloped, without prominent tail. Internal vein straight, or even a little bulging. Vein iii_3 arises a little beyond cross-vein, and herein is this form specialized.

The following type seems related to those immediately preceding:

Iliades memnon.

The fore wings are intermediate in shape between *Priamedes* and *Parides;* the apices are blunt, while the outer margin is nearly straight. The tailless hind wings have the outer margin very slightly scalloped. The venation generally agrees; the internal vein of secondaries is straight.

I have been unable to obtain material of the butterfly "*Troides helena* L.," which Scudder gives as the type of Hübner's genus *Troides*, Verz. 88, a generic name which has then apparently been wrongly used for the type *Ornithoptera priamus* L. Specimens of "*Papilio helenus*," received from Dr. Staudinger and examined by me, do not differ from *Menelaides polytes* in venation; the "tail" is merely a little longer.

The last type I have been able to examine is:

Troilides torquatus.

The neuration agrees in every detail with that of *Heraclides*

thoas, so that I cannot distinguish the two in any way, and I must suppose this generic title to be invalid.

In all these generic types of the *Papilio* group the third radial branch arises just opposite the point of junction of the discal cross-vein, with a tendency to remove beyond it. The progress of this branch along the radius, outwardly, may be apparently taken as an index of the specialization. In the Papilionides there is a general correspondence between the movement of this vein and the specializations of the abdominal field of the secondaries. The bending of the internal vein of hind wings is secondary in its nature, has been probably attained along divergent lines, and is a separate and well-marked feature in the specializations of the wings of the Papilionides.

The question as to the value of generic characters becomes simplified when we reflect that there is no criterion, save that of quantity, by which we can divide them from specific characters. For practical purposes it is well to break up such extensive genera as *Papilio*, and to do so we must take slighter variations as the basis of the division. It may be remembered that none of our categories could apparently exist except for "missing links," and our species thus appear as the momentary results of an average of arrested development, with wider or narrower breaks between them. This is one of the irrelevant generalities which it is well to bear in mind, in order to avoid insisting too categorically upon the absolute value of our divisions and terms.

The generic types above discussed appear to group as follows:

Iphiclides.	Papilio.	Lærtias.	Priamides.
	Jasoniades.	Menalaides.	Ithobalus.
	Euphœades.	Achillides.	Parides.
	Calaides.		Iliades.
	Heraclides.		
	= *Troilides*.		
	Orpheides.		
	Nestorides.		

Systematic Position of the Papilionides.

The argument as to the rank and position in the system of the Papilionides may be recapitulated here: All the generic types in the Parnassi-Papilionidæ that I have been able to examine have

vein "ix" of primaries well developed. This vein arises at base next to vii, runs outwardly and downwardly, in a more or less strongly given curve, to internal margin. I am inclined to regard this vein "ix" as the remnant of a longitudinal vein which has become shortened, in the same way as vii becomes shortened and bent on the hind wings of the Papilionides, and of which latter the stages between the long, straight vein and the shorter curved vein are extant. This vein "ix" is opposed in position to vein viii of the Hesperiades, which appears as a slender fork to vein vii at base and is more or less distinct in the Pieridæ, Limnadidæ, Heliconiidæ, Libytheidæ, Nemeobiidæ, Riodinidæ, Lycænidæ and Hesperiadæ. I have found traces of it in *Argynnis* and *Vanessa* among the Nymphalidæ proper, but no indication of it in the Agapetidæ. Where it is wanting in otherwise related forms I adopt the view that it has faded out. It has faded out, then, in *Morpho*, while the cubital cross-vein is persistent.

While vein "ix" appears to be a character of a primary nature, the hind wings of the Papilionides display two other features, which, since they recur in other butterflies or moths, may be considered as characters of convergence. These are the humeral cell and the single internal vein. The three neurational features of the Papilionides together are wanting in all other butterflies, but the single internal vein appears again in the Saturniades, the humeral cell in the Limnadidæ and Bombycides, while nowhere throughout the higher Lepidoptera, so far as I yet know, is the primary character of vein "ix" repeated. The ancestry of the Papilionides is not yet made out by the discovery of surviving forms.

It is impossible to leave the Papilionides in a classificatory position between the Blues and the Skippers, because such a position violates the integrity of the Lycænid-Hesperian branch. The diurnals, as a whole, are susceptible of a tripartite division upon the neurational characteristics. These three divisions are, severally: the Parnassi-Papilionidæ, the Pieri-Nymphalidæ, and the Lycæni-Hesperiadæ. The first of these is isolated by the presence of vein "ix," the last two have a common bond in the presence of vein viii of the fore wings. Therefore the value of the divisions is unequal, and the first outweighs either of the two latter. If the Hesperiades are, then, to be forced at any point to admit the Papilionides, that point might be selected between the Pieri-Nymphalid and Lycæni-Hesperid groups. But the principal

defense for such an interpolation would be the common survival of the cubital cross-vein, which the Parnassians have lost. This is distinct in the Papilionidæ, and more or less so in the Nymphalid group, in the Limnadidæ, Heliconiidæ and Morphidæ, these latter appearing to be otherwise specialized Satyrids. Thus this survival is shown in groups primarily differing in the presence of "ix" or viii on fore wings. I conclude, then, it is here an independent survival in unrelated groups. Nothing can show more clearly the overstress that has been laid upon the generalized features of the Papilionid wing than the demonstration that this residual character is shared also by the brush-footed butterflies, with which Mr. Scudder would head the sequence of the diurnals. There appears to be nothing in the neuration to contradict the monophyllism of the brush-footed butterflies, unless we are prepared to assume that the Agapetidæ and Morphidæ have parted with vein "ix" and not with viii.

The forked anal vein (viii) of primaries is absent in the Satyrids, and this feature seems, outside of the sexual character of the swollen veins (traces of which I meet in certain of the Nymphalidæ proper) and the generalized radius, to distinguish these from the Pierids. But the character is repeated in other groups of the brush-footed butterflies, and it seems impossible to find positive neurational characters upon which the Pieri-Nymphalidæ might be divided. And only the general pattern or plan of the veining—*i. e.*, the more parallel neuration and equal spacing, the retention of the middle median branch in position, an indisposition in the veins to approach and furcate—distinguishes the wings of the Lycæni-Hesperiadæ from those of the Pieri-Nymphalidæ. The Blues show a radial specialization on a wing which is fundamentally Hesperian. This points to the fact that the Lycænidæ and Hesperiadæ are members of a common phylogenetic branch, however remote the point of divergence may lie. I assume that this branch joins the main stem of the Pieri-Nymphalid butterflies, because in the Charaxinæ I find an approach to the separated longitudinal veins of the Hesperiadæ, while vein viii of fore wings of the Whites and brush-footed butterflies is repeated in the Lycæni-Hesperid group. Whether future studies in ontogeny render a presumed connection of the Papilionides with the Nymphalids entertainable or not, we are equally warranted, from the opposed directions of the last anal vein of primaries, in classifying the diurnals as either Papilionides or Hesperiades.

I conclude, then, that no sufficient reason can be shown for interrupting the sequence of what has been called the Macrolepidoptera, which all alike possess vein viii, and that for a group of butterflies having, on the contrary, vein "ix," the proper place in the system is by themselves at the commencement of the series. It must be recollected that our phylogenies are largely suppositional, and that, practically, whatever their origin, the diurnals should be kept together in collections and catalogues. No gain in scientific accuracy is attained in discarding the general lines of the Fabrician sequence of 1787. The correspondences of the Papilionides do not lie with the Hesperiadæ, as urged by Mr. Scudder, but with the Pieri-Nymphalidæ: the suspension of the chrysalis with the Pierids, the neurational analogies with the Nymphalids. If these are acknowledged as affinities, not as analogies, then there is also no sufficient reason for changing what is practically the best sequence and which has the advantage of being long accepted. It is an innovation to place the Papilionides between the Blues and the Skippers, and one which I show to be destitute of reason, from the neuration as well as from a weighing of the value of other features which appear on the surface to justify such a conclusion (see my papers in *Natural Science* for January and February, '98). It must, then, appear to me that no greater mistake has as yet been made in classifying the butterflies than that which associates the Swallowtails with the Skippers. And this is the main part of my argument, that whatever relationship may be made out for the Papilionides with the other butterflies, the connection of the Blues and the Skippers should not be disturbed by the Swallowtails being thrust in between them.

An unwarranted use of the terms "superficial" and "structural" has been repeatedly made in lepidopterological writings, sometimes for the mere purpose of invidious comparison. The assumed antithesis, as between classes of external characters, is entirely illusory. Uncritical studies of the shape of the genital pieces, as of any other of the appendages, lead to common and unsatisfactory results. I conclude that a phylogenetic classification cannot be reached until primary and secondary features are distinguished and the characters indicating relationship separated from those of convergence.

The neurational characters of convergence which appear in certain Papilionides, and again in groups of the Nymphalids, may

be summed up as follows: The first radial branch may intersect with subcosta (*Idaides* and *Anæa*); the cubital cross-vein or its traces occurs in both series (in the Nymphalids in *Limnas*, *Heliconius*, *Morpho*), while traces of the humeral cell of secondaries of the Papilionides are found in the Limnadidæ and Heliconiidæ. It is remarkable that just in these two latter families the resemblance is contradicted by the fact that both display the forked vein viii, in contradistinction to the downwardly curved vein "ix" of the Papilionides. It is this fact that allows me to consider the characters of resemblance as residual and common to the lepidopterous wing, and as undecisive of questions of a nearer relationship. These characters, the traces of the cubital cross-vein, etc., allow of the view that the Limnadidæ and Heliconiidæ retain primitive features and may more nearly represent early stages of the Nymphalids proper. Genera like *Dione* may supply a connection between the Heliconians and *Argynninæ* and render the view probable that the brush-footed butterflies are monophyletic.

Variability in the Veining.

I have shown (*Trans. Ent. Soc. Lond.* 1897, 342) that the variations in the neuration within the limits of a species take the same direction with those used to define distinct species or genera. In other words, they follow the chief directions which underlie most changes in the neuration. These latter lie in the breaking up of the median series and the suppression of the radial branches. For instance, in the five-branched forms of the Anthocharini there will be found a tendency to discard one vein in the direction of the four-branched forms of *Tetracharis*. In a variable species standing between *Euchlœ* and *Tetracharis* the disappearing vein may be discarded by anticipation (specialization) or retained by reversion (generalization). In *Pontia* we have the three-branched form definitely assumed, and we may consider that the ancestry of *P. daplidice* has passed through the *Euchlœ* and *Tetracharis* stages. In the same way the passage of *Mancipium* to a three-branched form is in process of accomplishment; sufficient material has not yet been examined of *brassicæ* to determine whether the short apical veinlet is discarded or not in the majority of individuals. In the *Zerynthianæ* we find individual variation in the direction of the breaking up of the median series; sometimes vein iv_1 ascends the radius; again, in generalized individuals, it retains its older position

on the cross-vein. It is a mistaken view to consider these variations "abnormal." They have a definite end and object, and show us how the changes in the venation have been slowly attained. All the species we take cognizance of are seemingly in a certain stage of progression, which temporarily assumes an apparent greater or lesser stability as the insect and its environment are equalized. In *Crinopteryx familiella* Spuler considers that we have a now variable form in the final stages of discarding the many-branched radius of the secondaries, thus showing us how the wing of *Eriocephalus* may have passed into that of the aculeate *Tineidæ*.

Conclusion.

I have taken the present opportunity to review my publications upon the neuration of the diurnals, to compare the figures again with the photographs and preparations. After supplying the missing details in the figures of *Parnassius apollo* (in which the lower incomplete margin of the humeral cell was omitted) and of *Heliconius antiochus* (in which the traces of the cubital cross-vein and internal vein were left out), I find nothing to add or alter. The method employed by me prevents errors of commission, but, owing to defects in the preparations, overlooked at the time, it has happened that the above details were not reproduced on the stone.

My studies were entered upon with the view of bringing our classifications into a nearer correspondence with a probable phylogeny. It was unexpected that the result was to confirm the general sequence of Linné and Fabricius, no less than that of the modern authors, Wallace, W. H. Edwards, the Catalogue of Staudinger, at least so far that we may commence with the Papilionides. Since the Parnassians belong beyond question to this stem, and are more specialized than the Swallowtails proper, we should begin with this family. I may reply to comparisons that have been made, that no results obtained in this way, as between ultimate specializations of the same organ in different groups of butterflies, can affect the phylogeny brought out by me. For this latter rests on the primary character offered by vein "ix," and not upon coincidences in ultimate structure, which are not exclusive, and may well have been independently reproduced upon separate phylogenetic lines. These are characters of convergence, and are not properly used as an index to relationship.

A review of the general neuration shows that the hesperid wing

is the simplest existent form with the veins all separate. A movement in specialization of the radial branches, normal with the lepidoptera, changes this wing into that of the lycænids. Both are now specialized and hardened types, and the position of the median branches has become so fixed that, in their specialization, the middle branch will not yield and submits to extirpation *in situ*. The condition of the hesperid wing is nearly reproduced in *Charaxes*, and proves that this was the original condition also of the Pieri-Nymphalid branch. It has been abandoned in specialization through the process of absorption and furcation of the veins; thus the hesperid type of wing becomes the unit underlying all the wing types of the Hesperiades. Into this group, so closed, and having the internal vein (vii) forked at base (viii), we can nowhere properly interpolate a group possessing an additional vein ("ix") and having no fork (viii) to the internal vein (vii), although, as a matter of theory, we may contend that the papilionid wing had also primarily separated veins.

I conceive, then, the Hesperiades to be monophyletic, a development of a single branch or stem of the lepidopterous tree, and as being independent of the Papilionides and their ancestry. As compared to the Papilionides, the rest of the butterflies are in the position of the Noctuid branch when compared with the Saturniades. This parallel is not a little exact. The development in evolutionary changes of the Papilionid wing is closely copied by the Saturniadæ, which have but one anal vein on hind wings. We have the same hollowing out of the inner margin in both groups among specialized forms. The Hesperiades resemble generalized moths in having two or more internal veins, and although these are convergent characters, not of phyletic value, they sustain the parallel. The exclusiveness of the Papilionides is supported by vein "ix" of primaries. When we take into account their total wing-structure, the idea that we have to do with a radically different development of the lepidopterous type becomes more and more reasonable. I separate, therefore, not the Hesperiadæ, but the Papilionides from the rest of the butterflies, and herein I differ from other authors, no less than from Comstock.

The general inequalities of all the specializations preclude, to a great extent, the question of rank, which practically becomes a matter of more limited importance within the confines of a single group. And I may repeat here, that the specializations of the

larvæ are neither homologous nor dependent upon the specializations of the imago. The external influences by which the different stages are surrounded are radically diverse. It is demonstrable that in *Apatela* the larvæ are more specialized, as larvæ, than are the moths, as moths. These latter are simple Agrotids, or Hadenids. The larvæ rank with the Arctians in specialization. Generic differences between imagos are not necessarily shown *also*, but may be displayed independently in the earlier stages of the insect. A specialized chrysalis may be attained by a form which, in the imago state, lags behind its fellows. I ventured first to give this view of the independence in specialization of the stages as early as 1876. Mr. Butler's paper on *Apatela* remains, at least, an exquisite satire on a generic classification from larval characters alone.

However, I seem to differ from Mr. Scudder (*Hist. Sketch*, 103), who holds that generic distinctions are as easily traced in the larva as in the imago, thus assuming a parity in specialization. Nevertheless, in the case of the forms of *Agrotis* Led., we may have moths which offer characters upon which generic distinctions have been founded, while the larvæ are so much alike that no such characters appear with them. And again we find species of *Apatela*, feebly differentiated in the imago state, proceeding from strongly diverging larvæ. The whole group of Acronyctid genera is held together by specializations of the larva alone. No intimate characters hold *Panthea* and *Apatela* united as moths, and here it seems possible that the larval specializations common to both are non-phyletic, convergent, they have been acquired along different routes, and thus the basis of the family Apatelidæ would be artificial. Where no such contradiction is offered the development may be assumed as monophyletic, the classification as natural. This view does not militate against the validity of Dyar's general classification as based on the larval tubercles in position. This character, as pointed out by me in '97, is valuable from its indifference to external influences.

In the case of the Papilionides there appears to be the alternative that either vein "ix" has developed subsequently to the disappearance of viii or before its appearance. If we accept the latter, then the Papilionides have branched off, as Prof. Comstock says, long before butterflies assumed their present form (*Evolution and Taxonomy*, 112). In this case all traces of an immediate ancestry

have, however, vanished. No concession to this fact is made by placing the Papilionides, as Prof. Comstock does, between the Blues and Skippers, clearly, even if distantly, related groups, offering at least no such contradictory characters as do the Swallowtails. Prof. Comstock in his able treatise, to which I am much indebted, does not entertain the view that the Papilionides may *not* have branched off from the immediate stem of the other butterflies, nor does he apparently insist upon the morphological value of vein "ix."

The diphylism of the diurnals is founded by me on the following characters:

A. Butterflies having a short anal vein on primaries, running from base to internal margin; on secondaries only one internal vein.....PAPILIONIDES.

B. Butterflies wanting the anal vein on primaries, instead vein vii is forked at base (viii), this fork sometimes wanting through degeneration, and having more than one internal vein on secondaries.....HESPERIADES.

All the Hesperiades examined by me have two internal veins to the hind wings, except *Pseudopontia*, which has three. This peculiar butterfly has the radius strongly specialized, and the retention of the third internal vein may have been necessitated by the circular shape of the wings. Theoretically it may be considered that all the diurnals possessed primitively three internal veins, in addition to the fold (vi), of which the Hesperiades, with the exception above noted, have parted with one, the Papilionides with two veins. In this particular the latter group are more specialized than all the other butterflies. The Saturniadæ, among the higher moths, have reached the same grade of specialization in this particular with the Papilionides. A diminution in the number of internal veins characterizes also certain of the more specialized groups of the Bombycides. The monotypic character of the Papilionides is evinced by the possession of vein "ix" of primaries, in which they appear to differ from all other butterflies, not by the number of internal veins, or by any other characters which they can be shown to share with other lepidoptera. Throughout my writings I have tried to show the direction of the evolution taken by the neuration, and I have accounted for the principal changes in position of the veins by their following these directions in spe-

cialization. The branches do not move backwards and forwards, but always tend to remove outwardly. None of these movements affect vein "ix." This remains stationary in the Papilionides, undisturbed by the changes in the radial branches, or of those marking the breaking up of the "median" system of the wing, as designated by Comstock.

For it does not affect the conclusions I have reached whether Comstock's nomenclature be ultimately adopted or not, while I favor its adoption. Whether the costal thickening be homologous with the veins, whether what I have called vein ii should not be rather called after Haase and Spuler vein i, or even whether Comstock's "radius" should be called the subcostal—and the "media," the radius—all these are questions of names and homologies with which my results are not primarily concerned. Whatever names are adopted, I believe to have shown that specializations are evidenced by the absorption of the veins, by the reduction of the radial (Comstock) branches and their progression along the main vein, by the opening of the discal cell and the fusion of the branches of the media (Comstock) with the radial or cubital systems of the wing. And whether we call the last, downwardly curved vein of the primaries of the Papilionides "anal," "internal," or "submedian," or number it, does in no way affect the argument, deducible from its presence, that the group possessing it occupies an exclusive position. I have further relieved the Papilionides from the vague charge of generalization, by showing that their residual characters are shared by the brush-footed butterflies, and that in the presence of but one internal vein to the secondaries they possess a character of specialization raising them above all the rest. Not the Swallowtails, but the Blues, are, from the neuration, the allies of the Skippers, and, having thus endeavored to divorce the Papilionides from their enforced association with the Hesperiadæ, I conclude that their fittest place is "at the head" of our linear systems and collections.

Finally (*Natural Science*, Feb., '98) I have ventured to suggest that certain changes in color run, in a general way, parallel with the specializations of the neuration. The white pigment colors appear to mark advanced forms. This is illustrated, in the Papilionides, by the fact that the Parnassiidæ, as a whole more specialized than the Papilionidæ, are also paler, more white in general hue. The most generalized group of the latter, *Ornithoptera*, contains species of the darkest, most intense coloration.

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Corrigenda.

To paper on the *Specializations of the Lepidopterous Wing; the Pieri-Nymphalidæ*, in these Proceedings, Vol. xxxvii, No. 157.

Page 23, line 6 from foot of page, *for* "Ager" *read* "Ageronians."

Page 24, line 25, *dele* the sentence commencing, "No trace of vein viii," etc.

Page 30, line 12 from foot of page, *insert* the words "a strong" before the words "vein viii of primaries."

Page 41, line 10 from foot of page, *for* "is" *read* "has."

Page 42, in the explanation of Plate I, Fig. 3 should refer to *Euchlœ cardamines*, Fig. 4 to *Anthocharis ausonides*. The numbers 3 and 4 are transposed on the plate.

Explanation of Plate III.

The figures are obtained by an improved photographic process. The veins are numbered according to the system Redtenbacher-Comstock: iii = radius, iv = media, v = cubitus. Vein "ix" of primaries, a principal character of the Papilionides, is numbered in red. The figures are of the natural size.

Fig. 1. *Parnassius apollo.*—Type of genus and family. The specialized form of the Papilionides, as shown by the following characters: On fore wings the first median branch (iv_1) has left cross-vein and arises from radius; the radius itself is four, instead of being five-branched; the cubital cross-vein has disappeared; on hind wings the lower margin of humeral cell has faded out superiorly, the internal margin is hollowed out, and vein vii is greatly shortened. *Doritis mnemosyne* does not differ generically from this type. *Hypermnestra helios* agrees by the four-branched, specialized radius, and I limit the subfamily to these two genera, since here the demarcation is abrupt, not, as in the Pierinæ, undefined.

Fig. 2. *Archon apollinus.*—Type of genus and belonging to the subfamily Zerynthianæ, of which it is the specialized form. Radius five-branched, generalized. The first median branch springs from cross-vein; lower margin of humeral cell complete; vein vii longer, as compared with *Parnassius*. The ornamental bands have not been broken up into the spots of *Parnassius*. The white color of the Parnassians and Pierids has been developed independently and is here a general character of convergence. *Archon* is seen to be a generalized form when compared with *Parnassius*.

Fig. 3. *Zerynthia polyxena.*—Type of genus and subfamily. Radius five-branched. In this species and its varieties vein iv_1, the first median branch, is in a fluid state, sometimes issuing from cross-vein, sometimes ascending radius. Compare figure of *Zerynthia rumina*, Schm. von Hildesheim, Taf. i, Fig. 2. Vein vii of hind wings is but little shortened.

Fig. 4. *Luehdorfia puziloi.*—Type of genus. Agrees well with *Zerynthia*. In both this and *Armandia* the cubitus shows a very inconspicuous scar, a relic of the vanished cubital cross-vein. The gradual disappearance of this cross-vein, from the Papilionidæ to the Parnassiidæ, demonstrates the greater specialization of the latter. Compare text.

Fig. 5. *Armandia thaitina.*—Belongs to Zerynthianæ. Type of genus. Radius five-branched; iv_1 from upper corner of cell. A beautiful and interesting form, owing to the papilionid shape of wings.

Fig. 6. *Sericinus telamon* ♀.—Type of genus. Radius five-branched. First median branch (iv_1) from cross-vein, and herein more generalized than *Armandia*. Vein vii of hind wings hardly shortened. Compare these Parnassian types with the ensuing Papilionidæ. Note the equal presence of vein "ix" of primary wings and the survival of but one anal vein (vii) on hind wings, and that the two types mainly differ in the breaking up of the median system in the Parnassians. It seems probable that, in extinct types of Papilionides, the vein "ix" was lengthened and sought the anal angle of the primary wing.

Explanation of Plate IV.

The figures are obtained by an improved photographic process. The veins are numbered according to the system Redtenbacher-Comstock: iii = radius, iv = media, v = cubitus. Vein "ix" of primaries, the principal character of the Papilionides, is numbered in red. The figures are of the natural size.

Fig. 7. *Teinopalpus imperialis* ♂.—Type of genus and family. The neuration is specialized, as compared with the Papilionidæ. The cubital cross vein is represented only by a residual mark. An intermediate type, with the breaking up of media on primaries taking the Parnassian direction, but an isolated offshoot from the Papilionid stem.

Fig. 8. *Leptocircus curius.*—Type of genus. A specialized form of Papilionidæ with the hind wing inferiorly enormously developed and the cell reduced.

Fig. 9. *Pathysa antiphates.*—Type of genus. On hind wing the discocellular cross-vein is downwardly bent between ii and iii. *Iphiclides* agrees with this type, except that the first radial branch is free. In *Pathysa* the first radial branch fuses with subcosta. Eimer, in his work, does not regard the neurational features of *Pathysa*.

Fig. 10. *Zetides sarpedon.*—Type of genus. Agrees in certain structural neurational points with *Pathysa*, differing by the inferior development and absence of "tails" and by the shorter anal vein of hind wings. This group is specialized by the inferior discontinuance of cubital cross-vein.

Fig. 11. *Arisbe similis.*—Type of genus. Agrees with *Zetides* in structural points, differing by the rounded hind wings. Compare text.

Fig. 12. *Eurycus cressida.*—Type of genus. Specialization is shown by the shortening of vein vii of hind wings and by the inferior degeneration of cubital cross-vein. *Eurycus* and *Pachlioptera* are interesting from the way they reproduce, upon a different type of wing, the specialization of the abdominal margin of the secondaries of *Parnassius*, a character of convergence, by which the margin becomes inwardly curved and the internal vein shortened. This direction crops out, among otherwise distinct forms, throughout the Papilionides. Again, as a character of convergence we meet it in the Saturniades (Grote, *Beitrag zur Class. aer Schm.*, S. 198, Fig. 1, *Callosamia*; S. 204, Fig. 9, *Rothschildia*; S. 206, Fig. 11, *Samia*).

Explanation of Plate V.

The figures are obtained by an improved photographic process. The veins are numbered according to the system Redtenbacher-Comstock: iii = radius, iv = media, v = cubitus. Vein "ix" of primaries, the principal character of the Papilionides, is numbered in red. The figures are of natural size, except Fig. 15, which is reduced one-half.

Fig. 13. *Iphiclides podalirius.*—Type of genus, to be compared with figure of *Pathysa antiphates.* Cubital cross-vein degenerates inferiorly. Between ii and iii of hind wings the discocellular is downwardly bent, as in the *Idaides* group. Radial branches free to costa, a character which brings this genus into the typical group of *Papilio*, with vein iii_3, the third radial branch, opposite cross-vein. Thus the genus is partly intermediate and appears, on the whole, nearer allied to *Idaides*, or rather to *Pathysa*, than to *Papilio.*

Fig. 14. *Priamides pompeius.*—Type of genus and belonging to typical group of *Papilio.* Compare text. [*Drurya antimachus*, mimetic of *Acræa*, not examined; probably belongs to the *Papilio* group as a specialized form.]

Fig. 15. *Ornithoptera priamus* ♂.—Type of genus. Note position of the third radial branch, which is thrown off before cross-vein. The furcation of iii_4 and iii_5 is long, so that the primitive condition which I assume, in which the longitudinal veins were all separate, is nearly attained. The total evidence is that *Ornithoptera* retains characters of the primitive form of the Papilionides. Compare wing with that of *Charaxes*, Schm. Hild., Taf. iii, Fig. 17, and Stein d. Weis., x, 282.

Fig. 16. *Heliconius antiochus.*—Type of genus and family. Belongs to the Hesperiades. Reproduced here to correct omissions in former figure; consult text. A more generalized form than the succeeding. Vein viii of fore wings partially degenerate; compare with figures of *Limnas* and *Libythea* in this respect, Proc. Am. Phil. Soc., xxxvii, Pl. iii.

Fig. 17. *Dione iuno.*—Generic type. Vein viii of primaries lost, but traces of cubital cross-vein retained. Belongs apparently to the Nymphalidæ. Consult figure of type in Proc. Am. Phil. Soc., xxxvii, Pl. ii. The open cell and condition of cross-vein on secondaries evidence the grade of specialization. Note that these figures of Hesperiades have two anal veins on hind wings, in contrast with the single vein of the Papilionides.

Fig. 18. *Tragonoptera brookeana.*—Section of ♂ primary wing, showing point of origin of third radial branch just before cross-vein. The position of *Papilio* has not been quite attained, while that of *Ornithoptera* has been abandoned.